蝶と蛾 *Trans. lepid. Soc. Japan* **48** (2) : 115–123, June 1997

Population interaction between aphidophagous butterfly, *Taraka hamada* (Lepidoptera, Lycaenidae) and its larval prey aphid, *Ceratovacuna japonica*

Hideo BANNO

9-20-42, Sagamioono, Sagamihara, Kanagawa, 228 Japan

Abstract The population interaction between aphidophagous butterfly, *Taraka hamada* and its larval food aphid, *Ceratovacuna japonica* was studied in the field. The numbers of the butterflies and aphids drastically changed every year. The aphid colonies increased from March and reached a maximum from late June to early July. The butterflies increased following the growth of aphid colonies and attained to a maximum number in early August. Aphid colonies decreased abruptly through July to August due to the intensive predation by the butterfly larvae. Thus, the butterfly larvae were faced with the food shortage, and consequently butterflies also decreased rapidly. The butterfly larvae entered overwintering diapause in late September, and stopped feeding on aphids. The characteristics of life histories of the butterfly and aphid were important for the maintenance of the predation-prey system between them.

Key words Population fluctuation, aphidophagy, *Taraka hamada*, *Ceratovacuna japonica*, predator-prey system.

Introduction

Taraka hamada Druce is a tiny lycaenid and is a unique obligate carnivorous butterfly in Japan. Larvae feed on the honeydew of aphids in early stage and later on aphids (Fukuda *et al*., 1972). In lowlands of the Kanto district, central Japan, they mainly feed on *Ceratovacuna japonica* Takahashi which is parasitic on the leaves of several species of bamboo and bamboo grass (Takahashi, 1958). Since adult butterflies also utilize the honeydew of this aphid as food, the distribution and abundance of the butterfly strongly depend on these of the aphid. The host plants of aphids are widely distributed but the aphids occur temporarily and locally. The habitat of this butterfly is, therefore, limited to some narrow places.

The previous studies of butterfly populations showed that the larval foods exert various influence on the population sizes of butterflies (Singer, 1972 ; Dempster *et al*., 1979 ; Ehrlich *et al*., 1980 ; Thomas, 1983 ; Arnold, 1987 ; Braby, 1995). In general, in predator-prey systems, as predators' number increases, the amount of prey decreases. Thus, the amount of prey also controls the number of predators. The food shortage may especially be serious in the predators which utilize the limited kinds of prey, because the species have small chance of change their food for other prey species. *T. hamada* is an almost monophagous predator in this study area. In order to know the relationship between this butterfly and prey aphid, the detailed field studies which extend over several years are necessary. The purposes of this study are : (1) to monitor precisely the populations of these species in the field and (2) to examine the maintenance mechanism of this predator-prey system.

Study site and methods

The study site was situated in Tsukuba City, Ibaraki Prefecture and was a pine forest (*Pinus densiflora* Sieb. et. Zucc.) about 62 m long and 5 to 8 m wide between the road and the

irrigation ditch. The forest floor was dominantly covered with the bamboo grass (*Pleioblastus chino* Makino), and *C. japonica* occurred on the underside of the bamboo leaves in several sizes of colonies. In addition to bamboo grasses and pine trees, many herbaceous and several woody plants were recognized in this site. There was no other occurrence place of *T. hamada* within a radius of 250 m from the study site.

The adult butterflies were counted during adult flight periods from May 1979 to September 1982 at intervals of about 10 days. Butterflies were captured in a hand net and stored in a small cage (25 cm in diameter and 30 cm in depth). After they were counted, they were released at the same site. The aphid colonies was counted from April 1979 to September 1982 at intervals of about 10 days from April to September and once a month from October to March. The aphid colonies were divided into five classes based on their sizes, and the amount of aphids was calculated by the mean dry weight of each class. At the same time, the larvae and pupae of *T. hamada* and the other predators of aphids were also recorded.

The influence of aphid amount on larval survival was studied in detail for two periods, mid to late July (aphid was abundant) and mid-August (aphid was few) in 1983. This was carried out in one place of study site, where the low density of plant allowed to observe the immature stages of butterfly. Eggs, larvae and pupae of the butterfly were observed and counted every one or two days.

The effect of predation by the larvae of *T. hamada* on the aphid population was examined from July to September 1984. Two places were selected in study site for this experiments. In one place, eggs, larvae and adults of *T. hamada* were removed everyday, and they were kept intact in the other place. The number of aphid colonies were recorded at intervals of 4 or 5 days in two places.

The population growth rate of aphids was studied in the experimental populations. The aphid colonies, which consisted of various instar nymphs, were transplanted to the bamboo grass planted in the pot. The increase of aphids was recorded while the density was below the carrying capacity. The population growth rate of aphids was determined by fitting the exponential growth curve, $N_t = N_0 e^{rt}$, in which t is the time interval (day), N_0 is the number of aphids at the beginning of the interval, e is a Napierian constant, and r is the population growth rate of aphid.

Results

The number of butterflies and the amount of aphids fluctuated on a large scale every year (Fig. 1). The 1st-brood butterflies were captured from May to June, but the number was small. The 2nd-brood butterflies emerged from late June to July with a small peak from early to mid-July. Afterward, butterflies rapidly increased and reached a maximum of the year in early August (except in 1981). Two generations overlapped after the 2nd brood. The maximum numbers were 140, 141, 56 and 75 in 1979, 1980, 1981 and 1982 respectively. During August, the number of butterflies rapidly decreased and eventually became very small in late August. The last adults were captured in late September (1979, 1980 and 1982), or in mid-October (1981).

Overwintered aphids increased slightly from April to May. Afterwards the aphids increased rapidly until early to mid-June, and then decreased or scarcely increased. After that time they increased again and attained to a maximum (except in 1979) during late June to early July. The maximum of 1979 was considered to be underestimated, because the census was

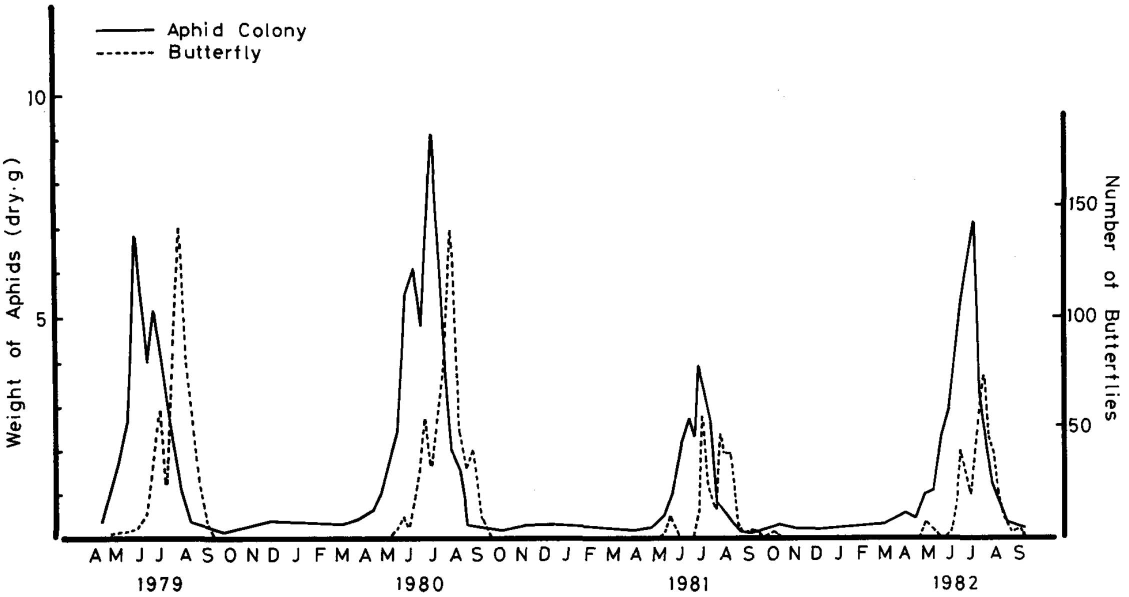

Fig. 1. Population fluctuations of *Taraka hamada* and *Ceratovacuna japonica* from 1979 to 1982 in the study site.

not carried out during the time (June 6–23) when aphids were probably most abundant. The aphids decreased precipitously during mid-July to late August, and then gradually declined till mid-September or October. In early October, some winged aphids produced from the colony. The aphids overwintered without remarkable change in their number.

It was difficult to find larvae and pupae of butterfly completely, because the bamboo grasses were thick and intertwined, and because the early instar larvae were lost among a crowd of aphids and the larvae pupated at various places. The 1st and 2nd instar larvae of *T. hamada* made silky nests in the aphid colonies. The 3rd and 4th instar larvae did not have the nests and fed on aphids moving from one aphid colony to another. The pupae were found on the underside on leaves of bamboo grass and of many other plants. The overwintered larvae grew from April to May, and pupated in May and then emerged as the 1st brood adult from May to June. The larvae from the 1st and 2nd brood butterflies were not abundant. After mid-July the larvae of two generations were observed at a time. The larvae were most abundant from July to mid-August, and fed on aphids intensively. After that they decreased in number rapidly. Almost all larvae were the 1st or 2nd instars in September, and passed through winter in the silky nests.

As the other predators on aphids, the larvae of a moth (Stathmopodidae), a brown lacewing (Hemerobiidae) and a syrphid fly (Syrphidae) were observed. The most abundant predator among them was the larvae of a stathmopodid moth, which appeared from mid-May to June, and were abundant from late June to early July, but in small numbers in August. The larvae of a brown lacewing and a syrphid fly were not abundant and were observed temporarily in each year.

The developmental process of immature stages of *T. hamada* from July 14 to 29 (when aphid colonies were abundant) is shown in Fig. 2 and from August 9 to 19 (when aphid colonies were not abundant) in Fig. 3. It was difficult to find and to count the eggs during the former period because they were often in a crowd of aphids. Thus, the eggs were not recorded during the period. In addition, since the 4th instar larvae dispersed at the time of pupation,

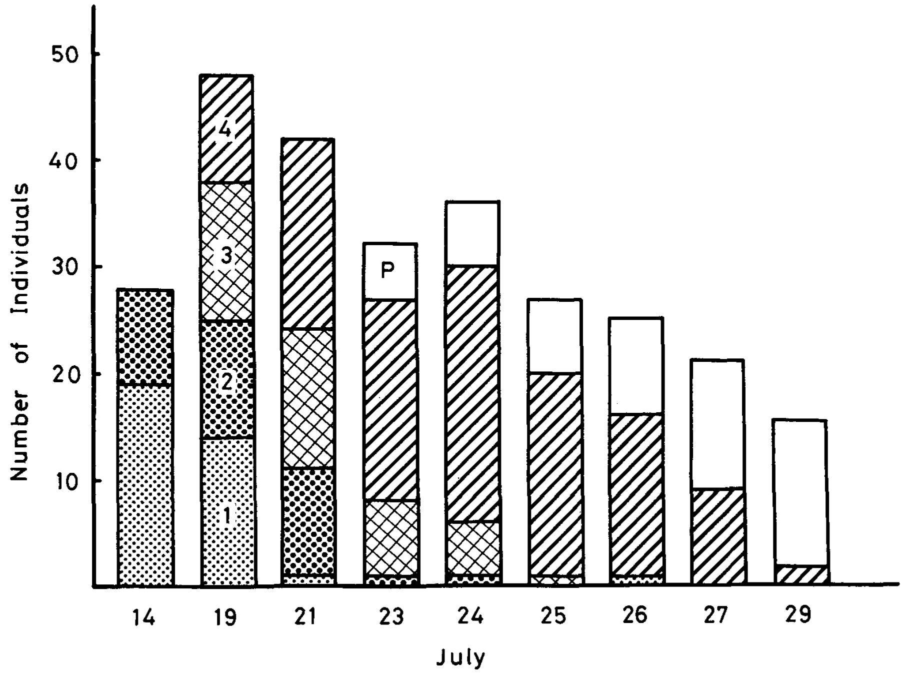

Fig. 2. The records of larvae and pupae in one low plant density area of study site from July 14 to 29 in 1983. 1 : 1st, 2 : 2nd, 3 : 3rd, 4 : 4th instar larvae, P : pupa.

all that were about to pupate could not be observed. On July 14 (the first day of study), all larvae were the 1st or 2nd instars. By July 24 (ten days after), many of them grew to the 4th instar or pupal stage. Although, as stated above, all of them could not be observed, the considerable number of the 4th instar larvae and pupae could be found. This indicated that most of larvae could pupate in this period. On the other hand, almost of all larvae could not grow up during the later period. Since the aphids had decreased, 54 eggs could be found during this period. By counting the eggshells, it was recognized that at least 48 of them hatched. However, only 13 1st instar larvae could be observed, and many larvae were considered to be unable to settle in the aphid colonies. The mortality of early stages was very high when aphid colonies were not abundant.

The changes in the number of aphid colonies in the experimental and control places are shown in Fig. 4. In the control place, there were about 90 aphid colonies at the beginning of this experiment (July 5). The moth larvae appeared in early July (9 individuals on July 5 and 11 on July 11), but their predation pressure was small. The aphid colonies increased in number and reached 160 on July 20. The larvae of *T. hamada* were observed after mid-July (9 on July 23). The aphid colonies rapidly decreased because on active feeding by the butterfly larvae, and the number of colonies fell to 9 on July 25. In the experimental place, 20 eggs, 73 larvae and 11 adults were removed during this experiment. The aphid colonies increased from July to August, and reached six times as many as initial number on September 3. The colonies decreased temporarily in early July and mid-August, because about 20 and 60 aphid colonies were crushed by the accidental invasion of a car at the respective days. The moth larvae were observed in late July and mid-August, and those of lacewing were also observed in late August. However, the predation by those larvae was not effective on the decrease of aphid colonies.

The r (population growth rate of aphid) was determined by using the regression equation, $\ln N_t = rt + \ln N_0$, and the r values of aphid are shown in Table 1. The r was similar in the

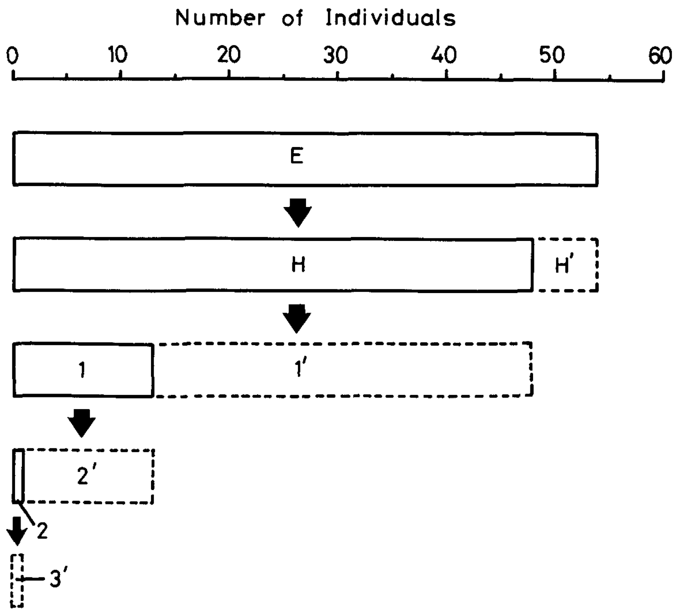

Fig. 3. The changes in the numbers of eggs and larvae in the same area of Fig. 3 from August 9 to 19 in 1983. E: egg, H: hatched egg, H′: disappeared egg, 1, 2: 1st or 2nd instar larvae, 1′, 2′, 3′: 1st, 2nd or 3rd instar larvae which were not recognized.

same periods in each year. The highest value was obtained during May to June and was 0.09–0.1. From July to September, the r was about 0.06–0.08. In April, November and December, the r values were low.

Discussion

It is reported that the population sizes fluctuate yearly or seasonally in other butterfly species (Ehrlich, 1965; Brown & Ehrlich, 1980; Ohsaki, 1982; Pollard, 1984). The larval food, parasitism and predation, disease and bad weather are thought as the factors affecting the fluctuation of butterfly population. The affects of food shortage on the population seem to be severe for the species which utilize the restricted kinds of plants. In many cases, the larval food shortage was attributed to the senescence of food plants owing to the bad weather conditions (Ehrlich *et al*., 1975, 1980). Dethier and MacArthur (1964) also reported that the population size of a nymphalid butterfly was affected by the decreasing in the amount of food plants with the succession of the old field. Since *T. hamada* utilizes the limited kinds of food, the number of emerged butterflies is considered to severely depend on the amount of foods.

T. hamada has five generations a year in the study area. In the multivoltine species of the temperate regions, the population size may fluctuate among generations. Their population sizes generally are considered to increase from spring to summer, because the most of them are phytophagous, and their larval food plants are usually stable during spring to summer. However, they usually do not increase absurdly, because the population size of them are often regulated by parasitic and/or predatory species (Bernstein, 1980; Hirose *et al*., 1980). The larvae of *T. hamada* attacked by predator was never recorded in the study site, despite the fairly long census time during four years. Although the 2nd instar larva attacked by the larva of Hemerobiidae was once observed in other place, the predation to the butterfly larva is considered to be small. The silky nests of young larvae may be useful in protecting them

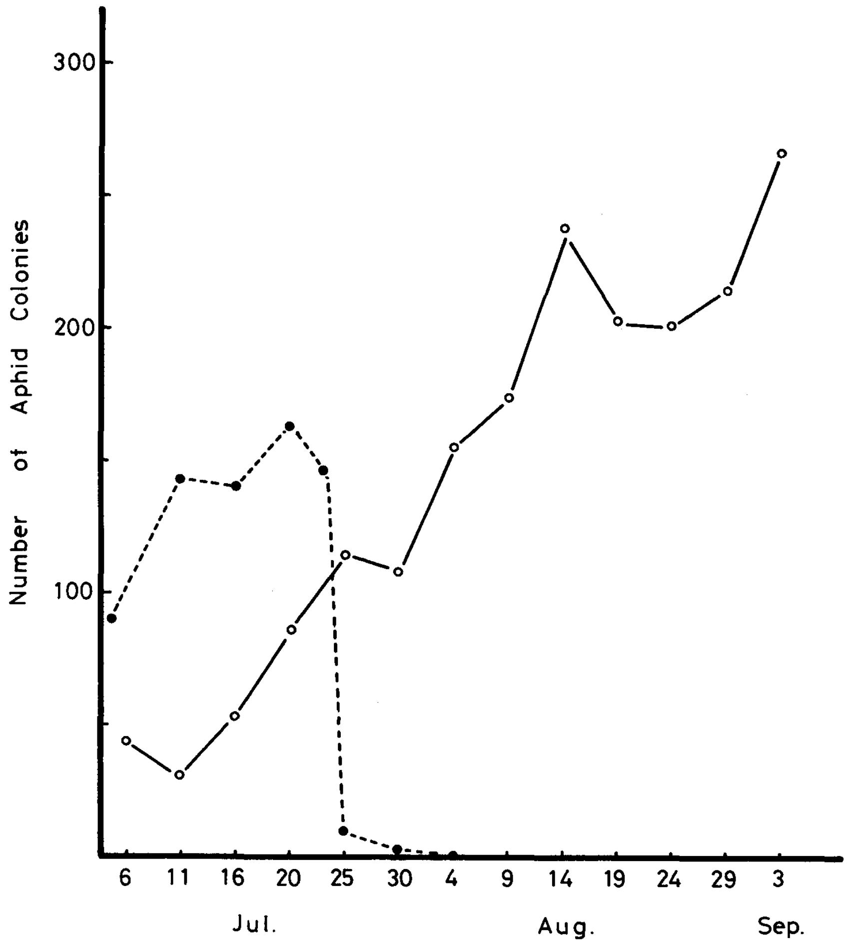

Fig. 4. The change in the number of aphid colonies in experimental (solid line) and control (broken line) places from July 5 to September 3, 1984.

from predators. Moreover, the larva of *T. hamada* is considered to have no parasitic species, because there was no parasitized individual among 160 larvae collected from several places other than this study site. Presumably, the larva of *T. hamada* is unpredictable resource for the parasitic species in both amount and distribution.

The present results lead to the coaction between *T. hamada* and *C. japonica*, as described below. The overwintered aphids begin to increase in early spring. On the other hand, the overwintered butterfly larvae start to feed on the aphids slightly after, but are small in number, and therefore the predation pressure on aphid is not high. Most of the overwintered larvae pupate by late May and the larvae from the 1st brood are still small in number, while the population growth rate of aphid is the highest of a year from May to June. Thus, the aphids are able to increase without the large damage by butterfly larval predation. The larvae from the 3rd brood are large in number and feed on aphids intensively, and consequently the aphids rapidly decrease through July to August. This predation brings about the food shortage for the butterfly larvae, and many larvae after the 3rd generation are considered to starve. The larval mortality of butterfly rises and its number decreases rapidly, even though the larva has physiological characteristics for food shortage (Banno, 1990*a*, 1990*b*). In late September, the early instar larvae of butterfly enter overwintering diapause, and the aphids are free from the predation pressure. After that, the aphids increase slowly from September to November, and overwinter without conspicuous change in number.

Table 1. The population growth rate of *Ceratovacuna japonica*.

Year	Period of experiment	Growth rate (r)
1977	Jun. 13–Jul. 11	0.098
	Jun. 13–Jul. 11	0.085
	Aug. 5–Sep. 5	0.070
	Aug. 20–Sep. 28	0.055
1979	Apr. 18–May 26	0.028
	Jul. 15–Aug. 20	0.092
	Sep. 1–Sep. 25	0.079
	Sep. 1–Sep. 29	0.077
	Oct. 28–Dec. 16	0.055
1980	May 19–May 31	0.108
	May 25–Jun. 22	0.122
1981	Jun. 4–Jul. 7	0.091
	Jun. 30–Aug. 2	0.070
	Jul. 18–Sep. 26	0.061

The small number of predator and the high population growth rate of prey in spring are necessary to keep up the predator-prey system of *T. hamada* and *C. japonica*. The stop of predation due to larval diapause is also important for the maintenance of this system. The aphids were not extinct by the predation of butterfly larvae in the study site, probably because this site was very large. The habitable places of *T. hamada* found usually are small, and only 20–40 butterflies were actually observed at the flight peak. The places are often disappeared by the extinction of aphids caused by the butterfly larvae. On the contrary, the new habitable places of the butterfly may appear by the dispersion of aphids. Banno (1988) reported that the butterflies moved to new places and produced offspring there. Thus, the immigration of winged aphids, which produce new suitable places for the butterfly, is also important for the system of these two species.

Acknowledgments

I thank Dr J. Mishima, Obirin University, for useful advice and encouragement throughout the course of this study.

References

Arnold, R. A., 1987. Decline of the endangered Palos Verdes blue butterfly in California. *Biol. Conserv.* **40**: 203–217.

Banno, H., 1988. Adult dispersal and exploitation of new habitat in the aphidophagous butterfly, *Taraka hamada* (Lepidoptera, Lycaenidae). *Tyô Ga* **39**: 235–240.

———, 1990*a*. Plasticity of size and relative fecundity in the aphidophagous lycaenid butterfly, *Taraka hamada*. *Ecol. Ent.* **15**: 111–113.

Banno, H., 1990*b*. Dry matter budget and food utilization efficiency of the larvae of aphidophagous butterfly, *Taraka hamada* (Lepidoptera, Lycaenidae). *Tyô Ga* **41**: 243–249.
Bernstein, C., 1980. Density-dependent changes in sex ratio in *Colias lesbia* (Lepidoptera: Pieridae). *Ecol. Ent.* **5**: 105–110.
Braby, M. F., 1995. Seasonal changes in relative abundance and spatial distribution of Australian lowland tropical satyrine butterflies. *Aust. J. Zool.* **43**: 209–229.
Brown, I. L. & P. R. Ehrlich, 1980. Population biology of the checkerspot butterfly, *Euphydryas chalcedona* structure of the Jasper Ridge colony. *Oecologia* **47**: 239–251.
Dempster, J. P., King, M. L. & K. H. Lakhandi, 1976. The status of the swallowtail butterfly in Britain. *Ecol. Ent.* **1**: 71–84.
Dethier, V. G. & R. H. MacArthur, 1964. A field's capacity to support a butterfly population. *Nature* **201**: 728–729.
Ehrlich, P. R., 1965. The population biology of the butterfly, *Euphydryas editha*. II. The structure of the Jasper Ridge colony. *Evolution* **19**: 327–336.
Ehrlich, P. R., White, R. R., Singer, M. C., McKechnie, S. W. & L. E. Gilbert, 1975. Checkerspot butterflies: a historical perspective. *Science* **188**: 221–228.
Ehrlich, P. R., Murphy, D. D., Singer, M. C., Sherwood, C. B., White, R. R. & I. L. Brown, 1980. Extinction, reduction, stability and increase: the responses of checkerspot butterfly (*Euphydryas*) population to the California drought. *Oecologia* **46**: 101–105.
Fukuda, H., Kuzuya, T., Takahashi, A., Takahashi, M., Tanaka, B. & M. Wakabayashi, 1972. Butterflies. *Insect's Life in Japan* **3**. xvi, 278 pp., 56 pls. Hoikusha, Osaka.
Hirose, Y., Suzuki, Y., Takagi, M., Hiehata, K., Yamasaki, M., Kimoto, H., Yamanaka, M., Iga, M. & K. Yamaguchi, 1980. Population dynamics of the citrus swallowtail *Papilio xuthus* Linne (Lepidoptera: Papilionidae) mechanism stabilization its numbers. *Researches Popul. Ecol. Kyoto Univ.* **21**: 260–285.
Ohsaki, N., 1982. Comparative population studies of three *Pieris* butterflies, *P. rapae*, *P. melete* and *P. napi*, living in the same area. III. Difference in the annual generation numbers in relation to habitat selection by adults. *Ibid.* **24**: 193–210.
Pollard, E., 1984. Fluctuations in the abundance of butterflies, 1976–82. *Ecol. Ent.* **9**: 179–188.
Singer, M. C., 1972. Complex components of habitat suitability within a butterfly colony. *Science* **176**: 75–77.
Takahashi, R., 1958. On the aphids of *Ceratovacuna* in Japan. *Kontyû* **26**: 187–190.
Thomas, J. A., 1983. The ecology and status of *Theymelicus acteon* (Lepidoptera: Hesperiidae) in Britain. *Ecol. Ent.* **8**: 427–435.

摘　　要

ゴイシシジミおよびササコナフキアブラムシ個体群間の関係（伴野　英雄）

ゴイシシジミと食物であるアブラムシとの関係を明らかにするために，野外における調査と実験を行なった．

調査地は茨城県つくば市にある道路と用水路に挟まれた細長いアカマツ林である．林床にはアズマネザサが生えており，ゴイシシジミの食物となるササコナフキアブラムシが寄生している．調査は 1979 年春から 1982 年秋まで行なわれた．週に一度の割でゴイシシジミ成虫の発生状況を記録した．また，アブラムシについては春から秋にかけては週に一度の割合で，冬期は月に一度の割合でコロニー数を調査した，このとき確認できたゴイシシジミの幼虫，蛹，ゴイシシジミ以外のアブラムシの捕食者についても記録した．1983 年の夏期には調査地内の観察のし易い場所を選び，アブラムシの多い時期と減少した時期でのゴイシシジミの幼虫の生存について追跡調査を行なった．さらに 1984 年に調査地の一部に，ゴイシシジミ除去区と非除去区をもうけゴイシシジミによるアブラムシへの捕食圧の検討実験を行なった．室内実験ではササの鉢植えを用い，アブラムシの季節ごとの増加率を調べた．

チョウの個体数およびアブラムシの量は季節的に大きく変動し，毎年同様の変化のパターンを示した．

越冬したアブラムシは3月頃より徐々に増加し始め，5-6月に急激に増加した．6月下旬にいったんピークに達するがその後一時減少し，再び増加して7月に最大となった．8月には急にその量は減少し9月にはピーク時の数十分の一程度にまでなる，その後少し増加し越冬に入った．冬期には量はほとんど変化せず翌春まで推移した．一方，ゴイシシジミは第一世代の成虫は5月より出現するが，個体数は少なかった．第二世代の成虫は6月下旬から7月上旬にかけて出現した．そして7月上旬から中旬にかけて最多になった．その後，成虫は急に増加し，8月上旬にはその年の最多になった．しかし，8月中に急激に個体数は減少していき，9月には少数の個体が見られるだけとなった．ゴイシシジミの幼虫の個体数は成虫の増加にともなって変化し，7月から8月に最も多く，アブラムシを激しく捕食した．9-10月になるとほとんどの個体は2齢で越冬に入り，アブラムシへの捕食は停止した．ゴイシシジミ以外にアブラムシの捕食者として，ニセマイコガ科の一種，ヒラタアブ，ヒメカゲロウの幼虫を確認した．ガの幼虫が6月にアブラムシの量にやや影響を与える以外は，これらのアブラムシに対する捕食圧は極めて小さかった．

ゴシシジミ幼虫の生存追跡調査より，アブラムシの多い期間には高い率で成虫まで生育するものと考えられた．一方，アブラムシの少ない期間では孵化した幼虫の内，成虫まで生育した個体はほとんどなかった．アブラムシに対する捕食圧を確かめる実験では，ゴイシシジミ除去区では8-9月でもアブラムシは増加した．一方，非除去区ではアブラムシは急激に減少し，ゴイシシジミの幼虫によるアブラムシに対するする捕食圧はかなり強力であると結論できた．アブラムシの個体群の増加率は5-6月が一番高く，初夏の急激な増加を可能にすると考えられた．

以上の結果から，本調査地におけるゴイシシジミとアブラムシの関係は次のように成り立っていると考えられる．越冬したアブラムシは3月頃より増加を始め，またゴイシシジミの幼虫もアブラムシを捕食し始める．しかし4-6月にはゴイシシジミの幼虫の個体数は少ないためアブラムシに対する捕食圧は小さい．一方，アブラムシは5-6月にその増加率が高く，急激に個体数を増加することが出来る．アブラムシはその後いったん蛾の幼虫の捕食により減少するが，再び増加し7月に個体数は最大になる．ゴイシシジミは徐々に個体数を増していき，第三世代の幼虫は個体数も多くアブラムシを激しく捕食するため，8月にはアブラムシは急激にその数を減少させる．アブラムシが減少するとゴイシシジミの幼虫は食物不足に陥り，生育できない個体が増えると考えられる．このような理由によりゴイシシジミの個体数は8-9月に急に減少する．9月になるとゴイシシジミの幼虫の多くはアブラムシの捕食を徐々に減らし越冬に入る．これによりアブラムシは捕食から解放され，食い尽くされずに残ったアブラムシは9-11月に少し増加し冬を越す．調査地で毎年観察された両種の個体数の大きな変化はこのような両種の関係で生じると考えられる．この関係が成立するためには，春から初夏にかけてのアブラムシの高い増加率と秋にゴイシシジミ幼虫が越冬のため捕食を停止することが重要であると考えられる．本調査地はゴイシシジミの生息地としては規模が大きく，アブラムシが食い尽くされずに毎年部分的に残った．しかし，よく見られる生息地は規模が小さく，1シーズン中にアブラムシの食い尽くしによる生息地の消滅が頻繁に見られる．ゴイシシジミは不安定な食物に依存し，生息地の消滅と出現を繰り返しながら個体群を維持していると考えられる．

(Accepted March 15, 1997)

Published by the Lepidopterological Society of Japan,
c/o Ogata Building, 2-17, Imabashi 3-chome, Chuo-ku, Osaka, 541 Japan